Pergamon

0042-6989(95)00341-X

Vision Res., Vol. 36, No. 19, pp. 3205–3227, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

Mach Bands: How Many Models are Possible? Recent Experimental Findings and Modeling Attempts

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Received 28 March 1995; in revised form 28 July 1995; in final form 15 November 1995

Mach bands are illusory bright and dark bands seen where a luminance plateau meets a ramp, as in half-shadows or penumbras. A tremendous amount of work has been devoted to studying the psychophysics and the potential underlying neural circuitry concerning this phenomenon. A number of theoretical models also have been proposed, originating in the seminal studies of Mach himself. The present article reviews the main experimental findings after 1965 and the main recent theories of early vision that have attempted to account for the effect. It is shown that the different theories share working principles and can be grouped into three classes: (a) feature-based; (b) rule-based; and (c) filling-in. In order to evaluate individual proposals, it is necessary to consider them in the larger picture of visual science and to determine how they contribute to the understanding of vision in general. Copyright © 1996 Elsevier Science Ltd.

Mach bands Brightness Lateral inhibition Filling-in Local energy Visual features

INTRODUCTION

Demonstrations of visual illusions abound in perception textbooks. The brightness illusion now referred to as Mach bands, after the Austrian scientist Ernst Mach who first studied it, is one of the most popular. This visual effect presents the classic case for distinguishing between physical and perceptual aspects of sensation. Regions of equal luminance appear vividly of different brightnesses and lines or bands appear where none are physically present in the stimulus (Fig. 1). In many instances, people have mistakenly interpreted such bands to be physically present in the images, as in the interpretation of clinical X-rays (see Ratliff, 1965, for examples). This one-to-many luminance to brightness mapping is common in many brightness phenomena (Todorović, 1987). Regions having identical luminances are perceived to be differently bright.

Mach bands are not only present in laboratory situations. They may be observed easily at the edge of virtually any shadow, where light and dark lines will surround the half-shadow (penumbra). While the scientific investigation of Mach bands was inaugurated by the studies of Mach in 1865, many artists have made use of the effect. Ratliff (1992) has demonstrated convincingly that they have been portrayed at least as far back as 1406 by the Flemish painter Robert Campin in his painting Annunciation (see p. 95 in Ratliff, 1992, for a reproduction).

Aside from being an excellent didactic tool for young students of perception, Mach bands have proven to be a very rich paradigm to probe early vision mechanisms. Mach bands have been used in order to investigate (a) the role of contours in perception; (b) the nature of lateral inhibition in the visual system; (c) the importance of phase information; (d) brightness perception; (e) the perception of lines and edges; (f) receptive field structure; and (g) linearity in the visual system, among other topics.

Historically, the most important contribution of the study of Mach bands was, perhaps, its role in the establishment of a close link between perception and underlying neural mechanisms. The studies of Hartline, Ratliff and colleagues (e.g. Hartline, 1949; Ratliff & Hartline, 1959) on the Limulus eye showed that responses of neural units (ommatidia) were interdependent. The results were interpreted in terms of lateral inhibition mechanisms. Ratliff and Hartline (1959) investigated the neural responses to a luminance ramp of the type known to elicit Mach bands and observed that the responses displayed activity undershoots and overshoots at the inflection points—i.e. the points where the ramp meets the plateaus ("knee" points). Linking such responses to the brightness undershoots and overshoots

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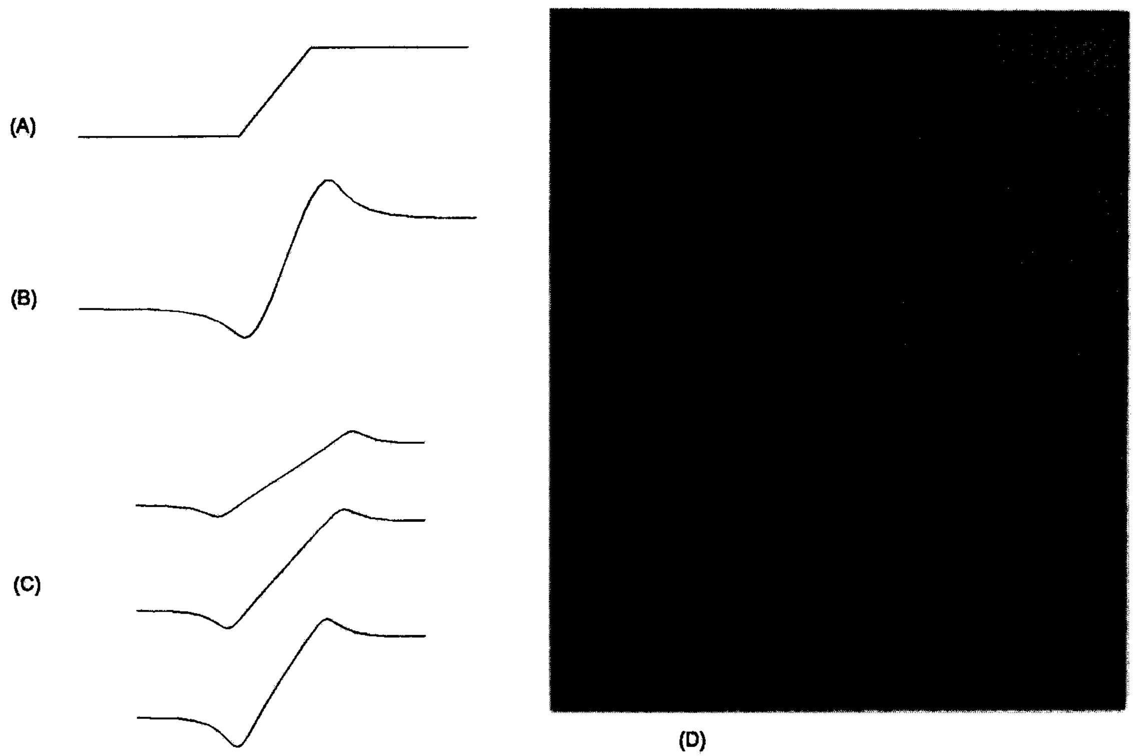

FIGURE 1. Mach bands. The profile in (A) represents a horizontal cross-section of the luminance distribution in (D). (B) Schematic representation of the perceived brightness. (C) Representation of the effect of gradient slope on Mach band appearance; slope increases from top to bottom.

that characterize the brightness distribution associated with such luminance ramps was irresistible. The study of Mach bands, therefore, provided one of the first cases of the successful* application of one of the most widespread linking hypotheses (Teller, 1980, 1984) currently employed in vision science: "We see X because elements Y at level L of the visual system are in state S" (adapted from Teller, 1990, p. 15).

Ratliff (1965) provides an excellent discussion of the literature on Mach bands, including the English translation of six original papers by Mach. Fiorentini (1972) also provides a very good review of the subject, including results between 1965 and 1972. Therefore, the review of the experimental literature will concentrate on more recent studies, discussing older results only when necessary to clarify more recent findings. A brief overview of earlier experimental findings and theories will be given in the next section in order to provide a historical background to the current investigations. More than a century of investigation has not yielded a definite answer concerning the mechanisms underlying Mach bands. As recently as 1983, one of the most prominent investigators of the effect has declared that "the one thing that is certain about them now is that we have no clear understanding of them" (Ratliff *et al.*, 1983, p. 4558). This article will attempt to summarize the key recent experimental findings on Mach bands as well as describe the main vision theories that attempt to model them. The literature on Mach bands in other scientific and technological lines of investigation will not be discussed. For example, the study of Mach bands is relevant from clinical dermatology (Shriner & Wagner, 1992) to computer graphics (e.g. Hodgkinson & O'Shea, 1994).

*To the extent that perceptual and neural events seemed to closely match, the linking was successful. However, the issue of the neural basis of Mach bands is far from being resolved and is the object of current investigation. Moreover, the studies with *Limulus* implied that Mach bands would be seen on luminance steps. These are rarely seen, as discussed at length in this article.

BRIEF REVIEW OF CLASSICAL RESULTS AND THEORIES

Experimental results

Mach bands were first qualitatively described by Mach (1865). The first quantitative measurements were reported in a series of investigations by Fiorentini and colleagues 90 yr later (e.g. Fiorentini, 1957; Fiorentini & Radici, 1957, 1958; Fiorentini *et al.*, 1955). A large fraction of the early studies on Mach bands investigated the influence of the slope of the gradient between uniform fields on the appearance of the bands. These studies measured either the apparent brightness or the width of the bands, or both. The results can be summarized as shown in Fig. 1(C). Increasing the slope of the gradient produces brighter and thinner light bands, and darker and more distinct dark bands. However, when the gradient

FIGURE 2. Schematic representation of early models of Mach bands. Left: luminance ramp distribution. Middle: center-surround or lateral inhibition weighting function. Right: output of the convolution of the luminance distribution and weighting function. Mach bands can be associated with the undershoots and overshoots in the output distribution.

becomes a luminance step, both light and dark bands *disappear* (Ratliff, 1965, p. 60).

Theories

Ratliff (1965) reviews six mathematical models of early visual processing that had been applied to Mach bands, including Mach's own proposal. Ratliff (1965, p. 120) concludes that the six models are basically one and the same and provide different instantiations of neural mechanisms of distance-dependent excitation and surround inhibition. While five of the models were proposed after Hartline's pioneering description of the center-surround receptive field of "optic nerve fibers" (Hartline, 1940), Mach's (1865) proposal was derived from his psychophysical experiments with gradient patterns, suggesting to him that the light and dark bands that now carry his name were produced by retinal distance-dependent lateral interactions.

In summary, the main models of Mach bands proposed by 1965 could all be described as relying on lateral inhibitory operations of the type now commonly associated with the function of, say, retinal ganglion cells (Fig. 2). Moreover, all of these models assumed that Mach bands were the result of retinal processing, not of later stages of the visual system.

RECENT EXPERIMENTAL RESULTS

Luminance steps induce weak Mach bands, if any

One hundred years after Mach described the effect that we now call Mach bands, the major theoretical explanations of the phenomenon involved lateral inhibition (Ratliff, 1965). Yet, no experimental evidence for the effect existed in the case where the luminance transition between the two plateau regions is a step. Such abrupt transitions should, of course, produce maximally strong effects according to lateral inhibition. This contradiction is puzzling. Ratliff (1965, p. 60) states that Mach bands do not occur when the slope of the luminance ramp is very small or very large. He then proceeds to review the major theories of the effect at the time and conclude that they all involve lateral inhibition. Giants of the field such as Mach, Békésy, Hartline and Ratliff, to name a few, could not have missed such contradiction. Perhaps some of them were convinced that Mach bands also would be exposed at luminance steps with the proper experimental procedures. This may be the case especially for Békésy,

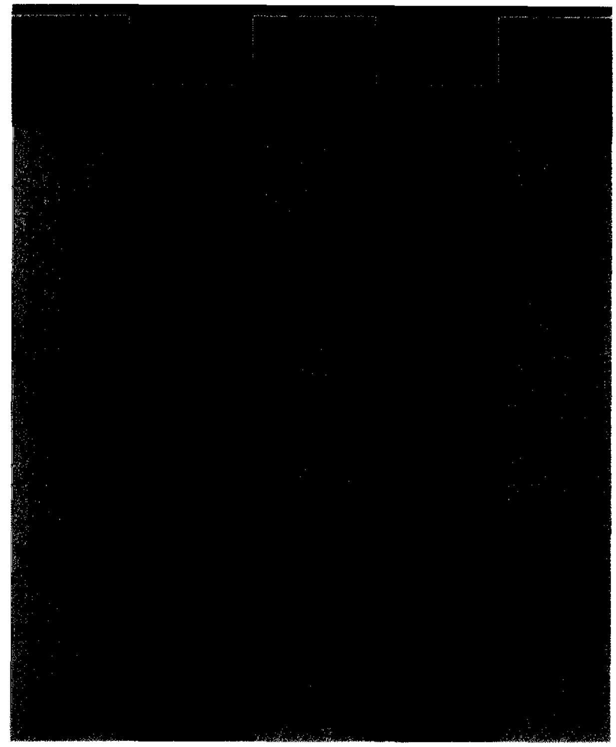

FIGURE 3. Square-wave modulation of luminance. The one-dimensional cross-section of the luminance distribution is shown on top. No Mach bands are seen.

who eventually provided some evidence in favor of this view (Békésy, 1968a).

Alternatively, the power of the theoretical approach in providing *qualitative* explanations for several phenom-

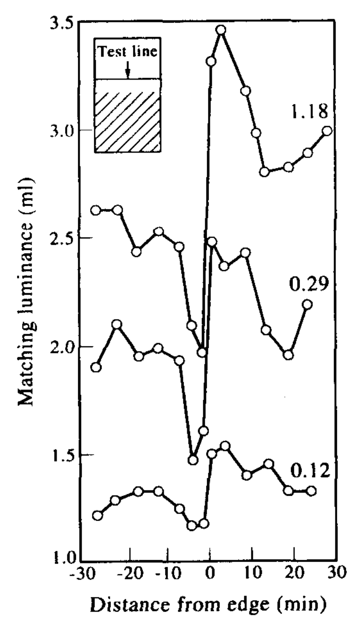

FIGURE 4. Experiment by Heinemann (1972) determining the distribution of brightness across a bipartite field. Luminance matches are plotted as a function of the distance from the edge. The curves are for three contrast levels used. Reprinted from Heinemann (1972) with permission.

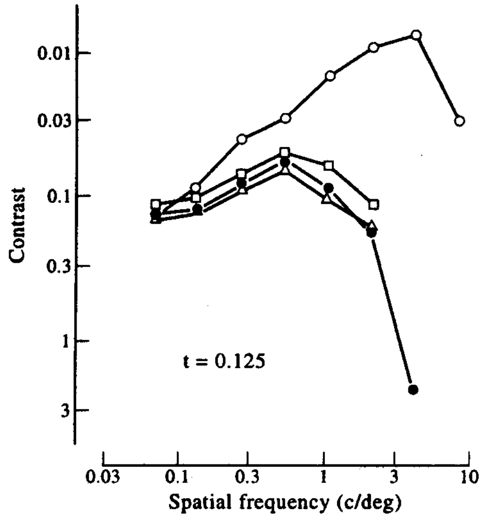

FIGURE 5. Threshold contrast for seeing light and dark Mach bands (open triangles and squares, respectively) as a function of spatial frequency (c/deg). Thresholds for detecting the residual waveforms as spatial frequency is varied are also shown (filled circles). Results from Ross *et al.* (1989) adapted with permission.

ena concerning perceived brightness and in *uniting* certain aspects of physiology and perception was deemed more important or compelling than such "exceptions". The type of model illustrated in Fig. 2 was used to explain (some properties of) brightness effects such as Mach bands, Hermann grids and the Craik–O'Brien–Cornsweet effect (Craik, 1940; O'Brien, 1958; Cornsweet, 1970); see Fiorentini *et al.*, 1990). At the same time, it provided good fits to neurophysiological data, such as the responses of the Limulus eye (Ratliff & Hartline, 1959) to both step and ramp luminance transitions (with undershoots and overshoots), and the responses of ON-center OFF-surround retinal ganglion cells of the cat (Enroth-Cugell & Robson, 1966). Nevertheless, this theoretical framework encountered problems when attempting to provide *quantitative* fits to brightness data (see Fiorentini *et al.*, 1990).

Evidence for Mach bands on luminance steps. Figure 3 shows a square-wave luminance modulation. Most observers find no traces of Mach bands in this stimulus. Could more careful investigation of the brightness variation across the figure reveal the effect? Heinemann (1972) and Békésy (1968a) suggest that this is the case (see also Matthews, 1966).

Figure 4 shows the results reported by Heinemann (1972) for the distribution of brightness across a bipartite field. The inset illustrates the paradigm used. A thin line of luminance L_t was placed at one of a series of positions in the bipartite field of luminance L_i as shown. L_t could be varied so as to appear darker or brighter than its background. The bipartite field with the superimposed line was presented to one eye. Given a fixed L_t, the subject's task was to adjust the luminance of a similar comparison line shown on an evenly illuminated background to the other eye, so that the two matched in brightness. Figure 4 shows the matching luminance as a function of the distance from the edge. The angular distance from the edge to the point at which the brightness first levels off is of the order of 10–15 arcmin. Heinemann states that the overshoots and undershoots observed in his data are light and dark Mach bands, respectively. His interpretation of the data implies rather broad Mach bands, although, as Heinemann states, they cannot be compared directly to widths determined by pointer settings without knowing where along the brightness curve the subject chooses to position the pointers. Mach bands originating from luminance ramps are typically thinner, on the order of from 3–5 (light bands) to 6–8 (dark bands) arcmin. Depending on the shape of the luminance distribution, they can go up to 10–12 arcmin (Fiorentini, 1972).

Heinemann acknowledges that his results are contrary to reports by other investigators. A discussion of such inconsistency is not provided aside from noting that "the problem of the appearance of uniform fields is complicated" (Heinemann, 1972, p. 163).

Békésy (1968a) also investigated the spatial distribution of brightness for luminance steps. With a flicker photometry method, he obtained evidence for brightness overshoots and undershoots at the light and dark sides of the step, respectively. The overshoots were more pronounced than the undershoots, consistent with several reports on luminance ramp Mach bands. Both overshoots and undershoots extended roughly 8 arcmin. Békésy (1968a) describes the brightness variation induced by the luminance step in terms of Mach bands and does not discuss any possible differences between ramp and edge stimuli.

Davidson (1966) (reviewed by Cornsweet, 1970) investigated the brightness of several luminance distributions, including regions of uniform luminance surrounded by steps. All patterns were of low contrast, and briefly flashed. Subjects were asked to judge whether the center of the stripe was brighter or darker than the region just to the side of the edge of the stripe. Under these conditions, a physically uniform stripe always appeared brighter at its edges. A stripe appeared uniform in brightness when the center region was of a higher luminance, and luminance decreased towards the (smooth) "edge". In other words, brightness overshoots at the region of the edges were determined with this experimental procedure. Are these light Mach bands? Davidson's (1966) investigation was not directed at the study of Mach bands, but instead aimed at determining whether the modulation transfer function (MTF) approach could account for certain aspects of brightness perception. His results, in fact, are well matched by the MTF, and can be generated by a system having lateral inhibition (see, e.g. Davidson, 1968). An MTF or lateral inhibition approach predicts that overshoots and undershoots will be associated with luminance steps, thereby predicting Mach bands for these stimuli.

Evidence against Mach bands on luminance steps: Dependency on spatial frequency and minimal ramp

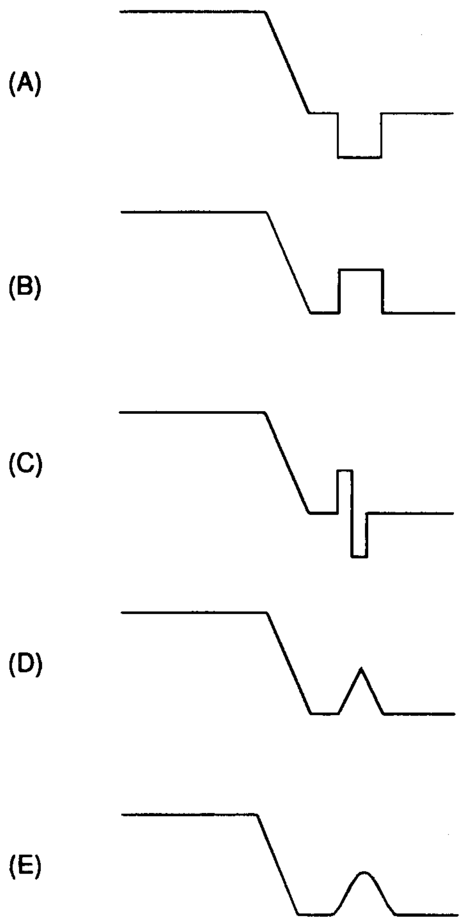

FIGURE 6. Cross-sections of patterns (A–E) employed by Ratliff *et al.* (1983) to study the effect of adjacent stimuli on Mach bands. Bars of sufficient contrast and sufficiently close to the ramp inflection point destroyed the adjacent Mach band. A triangular shaped adjacent stimulus (D) enhanced Mach bands, while a Gaussian shaped stimulus (E) had little or no effect.

width. Despite the evidence cited above, recent studies have challenged the existence of Mach bands at steps. Ross *et al.* (1981) used trapezoidal waves in order to investigate the visual system's sensitivity for seeing Mach bands as a function of spatial frequency and ramp width. In one experiment, they measured the contrast required to see Mach bands in gratings having equal plateau and ramp widths. For spatial frequencies above 2 c/deg, Mach bands were not visible even with the maximum contrast available for the equipment. Therefore, with their set-up, ramp widths of less than around 7.5 arcmin produced no Mach bands.

Ross *et al.* (1989) studied the threshold for seeing Mach bands in waveforms of different shapes (e.g. triangular, trapezoidal). For all shapes, sensitivity rose gently to a peak and then dropped sharply as spatial frequency increased (Fig. 5). The "inverted U" behavior for seeing Mach bands (for all shapes) demonstrated that ramps of intermediate width were optimal. Both narrow and wide ramps decreased Mach band visibility. Moreover, Mach bands ceased to be visible at a ramp width (given by the limiting frequency) around 4 arcmin.

Dependency on adjacent stimuli

Ratliff and colleagues (Ratliff *et al.*, 1979, 1983; Ratliff, 1984) followed Mach's (1906) idea of investigating the appearance of Mach bands by altering the spatial pattern of illumination adjacent to them. Their main finding was that the appearance of Mach bands was modified by placing stimuli, such as a bars, nearby. For certain stimulus conditions the bands disappeared altogether. Figure 6 shows one-dimensional cross-sections of the main luminance profiles used by Ratliff *et al.* (1983). Most of the adjacent stimuli were bars varying in direction of contrast, amount of contrast, proximity to the inflection points of the ramp, and width. Biphasic bar stimuli, as well as triangular and Gaussian-shaped stimuli, were employed also.

The findings of Ratliff *et al.* (1983) can be summarized as follows. (a) A bar stimulus of sufficient contrast placed near either inflection point attenuates the *adjacent* Mach band that normally is perceived at the inflection point; if the bar is positioned close enough, no Mach band is perceived. (b) A bar far away from the inflection point has no effect on Mach band appearance. (c) Attenuation is largely independent of the width of the adjacent bar stimulus. (d) Attenuation is largely independent of the *sign* of contrast of the bar. (e) A triangle-shaped stimulus near the inflection point enhances the nearby band; as the stimulus is moved and its associated Mach band approaches the stationary Mach band in the ramp pattern, one induced band fuses with the other and produces an enlarged Mach band. The enhancement occurs as long as both Mach bands are of the same polarity (light or dark). In the case where they have opposite contrasts, they attenuate each other. (f) A truncated Gaussian stimulus with the same area as a bar stimulus that attenuates a Mach band and that of a triangular stimulus that enhances a Mach band has little or no influence on Mach band appearance. In summary, the three main features of the interfering stimuli are *proximity*, *contrast* and *sharpness*.

Ratliff (1984) extended the results of Ratliff *et al.* (1983) by using biphasic bars [see Fig. 6(C)] positioned in the middle of the luminance ramp. Since the attenuation results observed by Ratliff *et al.* (1983) did not extend beyond around 15 arcmin, he employed a very

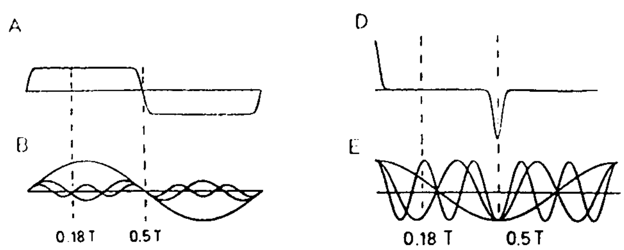

FIGURE 7. Illustration of phase congruence. The three first harmonics of a smoothed square-wave (left) and a series of delta functions (right) are shown below the respective one-dimensional luminance distributions. Note that at the edge (the mean luminance cross-over) and at the bar the phases of the three harmonics shown come into register. From Burr and Morrone (1992) with permission.

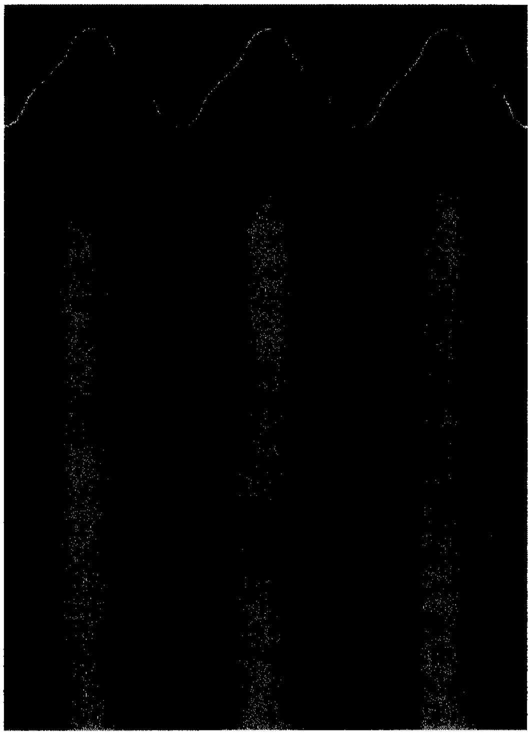

FIGURE 8. Example of the effect of the manipulation of the Fourier spectrum of a trapezoidal wave. All components have been shifted in phase by $\pi/2$. The one-dimensional cross-section of the luminance distribution is shown on top. No Mach bands are seen.

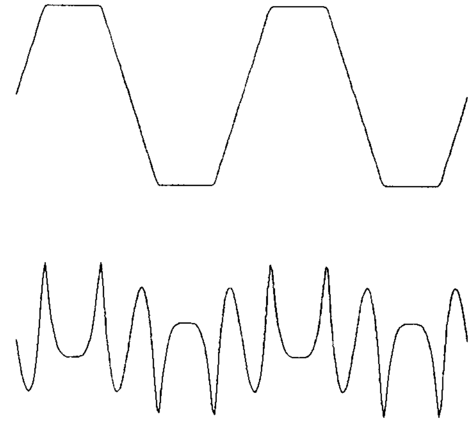

FIGURE 9. Luminance distribution for trapezoidal and associated residual waveforms used by Ross *et al.* (1989) to study phase information and Mach bands. Detection thresholds for residual waveforms follow the thresholds for seeing Mach bands very closely (see Fig. 5).

narrow ramp (15 arcmin). He showed that as the contrast of the biphasic bar was increased both light and dark band width decreased.

A recent investigation comparing Mach band attenuation for bars and stimuli defined by Craik–O'Brien "cusps" showed that both types of stimuli are equally effective in attenuating the bands (Pessoa, 1996). The findings suggest that the high-frequency components of an adjacent stimulus are responsible for the attenuation.

Dependency on spatial phase

Morrone *et al.* (1986) and Ross *et al.* (1989) have suggested that Mach bands depend on phase relationships among Fourier components of the underlying waveforms. Figure 7 shows the first three components in the Fourier expansion for a square-wave and a series of delta functions. In both cases, these harmonics (and all higher harmonics) come into phase periodically, at twice the frequency of the fundamental. At the square-wave edge location, all harmonics have phases $\pm\pi/2$ (assuming a cosine Fourier expansion), depending on the polarity of the edge. For the delta function (or bar), all harmonics have phases 0 or π at the peaks (again depending on polarity). Therefore, the edge and the bar (or band) correspond to the points of maximum phase congruence. Morrone and Burr (1988) have proposed that such points always mark visually salient features (see discussion on the local energy model below).

Morrone and colleagues noted that while the edge of a square-wave has the Fourier components coming into register with a phase of $\pm\pi/2$ (see Fig. 7), the components of a triangle-wave come into phase at the spatial locations corresponding to the luminance peaks of the waveform where the arrival phases are 0 for positive peaks and π for negative peaks. For a trapezoidal wave, the Fourier components never all come into phase exactly, but phases are most similar at the positions where the ramps meet the plateaus, where they are 0 and π, as in the triangular wave. A phase grouping of 0 and π is typical of that produced by bars (or delta functions as shown in Fig. 7) and Morrone and colleagues hypothesize that it may be the signal that produces or is associated with Mach bands.

The relationship between phase and Mach bands as proposed by Morrone and colleagues is illustrated by considering the stimulus in Fig. 8, showing the effect of manipulating the phase spectrum of a trapezoidal wave. For this stimulus, all components have been shifted in phase by $\pi/2$ to produce the Hilbert transform of the trapezoid. No Mach bands are seen and the pattern appears to have sharp transitions (edges), although no corresponding abrupt luminance changes are present at those locations. Edges are seen at the points where Mach bands appeared on the original trapezoidal waveform. The average phase at these points is $\pm\pi/2$, which is characteristic of edges, instead of 0 or π as in the trapezoidal wave which is characteristic of bars, demonstrating the importance of phase information in brightness perception.

Ross *et al.* (1989) studied triangular and trapezoidal waveforms and determined contrast thresholds for seeing Mach bands. They also measured contrast thresholds for *detecting* "residual waveforms" which were constructed from the triangular and trapezoidal waveforms by removing the first block of harmonics with $\pi/2$ phase (Fig. 9).* Residual waveforms were studied to clarify the

*For example, the first and third harmonics were removed from certain trapezoids.

relationship between phase information and Mach bands. Note that when the residual waveform is just undetectable, all remaining detectable components of the waveform have phase $\pi/2$ at the mean luminance cross-over point (these have actually been removed from the stimulus), which is characteristic of edges (see Fig. 7). It is assumed here that the visual system is behaving linearly; the first block of harmonics has higher amplitude and therefore should have been detectable if present. As the stimulus contrast of the residual waveform is increased and the higher harmonics become visible (their amplitudes are sufficient to elicit detection), phases become more similar at the positions corresponding to where the ramps meet plateaus where phases average 0 or π as in a bar; remember again that the first block of components with phase $\pi/2$ is not present in residual waveforms. Therefore, the prediction is that the threshold contrast for detecting residuals should be very similar to the threshold contrast for seeing Mach bands since both depend on Fourier components with phases 0 or π. Figure 5 (filled circles) shows that sensitivity for detecting residual waveforms follows rather closely thresholds for seeing Mach bands, confirming Ross and colleagues' prediction. These authors suggest then that Mach bands are visible on trapezoidal and triangular waveforms if the corresponding residual waveforms are independently visible.

Dependency on low-pass filtering

Ross *et al.* (1989) also investigated the effect of low-pass filtering on contrast thresholds for seeing Mach bands. The filter employed was a Gaussian of variable frequency constant. The contrast required to see light and dark Mach bands was measured at each of a range of cut-off frequencies of the filter. As the cut-off frequency of the Gaussian filter increases, the trapezoidal luminance waveforms are subject to less and less blurring—the inflection points become "sharper". Accordingly, Ross (1989) reported that as the cut-off frequency of the filter increased, sensitivity for seeing Mach bands increased.

Dependency on adaptation state

Békésy (1968b) studied the appearance of Mach bands for the dark-adapted eye. He employed a trapezoidal modulation of luminance and studied the qualitative appearance of the bands as a function of exposure duration following the period of dark adaptation. For exposure durations of less than about 0.125 sec, no Mach bands were seen. For exposure durations of 2 sec, two weak light Mach bands appeared. For longer exposure times (10 sec), the two light bands remained of the same brightness, but the ramp and low luminance plateaus became darker, producing narrower and more pronounced light Mach bands. Békésy (1968b) concluded that the brightness of the light Mach band seems to vary little with light adaptation–exposure time after dark adaptation.

The experiments reported above by Ross *et al.* (1981) were also performed in the dark adapted state. In this case, Mach bands were never seen (regardless of spatial frequency). According to Ross *et al.*, their patterns always appeared as undistorted light and dark plateaus separated by a ramp. Although details are not provided, the results of Ross *et al.* were obtained probably while subjects were still dark-adapted—thus, consistent with the observations of Békésy (1968b).

Second-order Mach bands

Phenomena that are elicited when the spatial variation of luminance is replaced with a spatial variation in contrast are called second-order phenomena (e.g. Chubb *et al.*, 1989; Singer & D'Zmura, 1994). In such studies, stimuli are generated by appropriately defined texture patterns. Recently, Lu and Sperling (1995) have demonstrated the occurrence of Mach bands in second-order stimuli that have ramp modulations of contrast while maintaining constant mean luminance. Their stimuli exhibited perceptual Mach bands that were decreases or increases in apparent texture contrast with no concomitant change in apparent brightness. Moreover, the magnitude of the second-order illusion was found to be similar to the classical luminance version.

Lu and Sperling also attempted to determine whether the second-order illusions depend on full-wave or half-wave rectification. In other words, they were interested in establishing the nature of the early non-linearities involved in the illusion. Full-wave rectification is usually assumed to be the absolute value or the square of point contrast. In half-wave rectification, there are commonly two half-wave processes, one positive and one negative. For example, ON-center retinal ganglion cells perform positive half-wave rectification, transmitting information primarily about luminance increments. OFF-center cells are analogous to negative half-wave rectifiers as they transmit information mainly about luminance decrements.

Lu and Sperling also demonstrated second-order versions of the Chevreul illusion (see below) and the Craik–O'Brien–Cornsweet effect. Since none of these illusions could be perceived with half-wave textures, they suggest that second-order illusions result from full-wave, not half-wave, rectification and involve spatial interactions that are rather similar to those in first-order (luminance) processing.

Mach bands and color

There is no general agreement on the appearance of Mach bands in pure color (isoluminant) stimuli. Several reports have claimed that the chromatic analog of Mach bands does occur, although these have been contested as possibly due to luminance differences. The current weight of consensus favors the view that chromatic Mach bands do not occur. The interested reader may consult Pease (1978) for a short review and Gur and Syrkin (1993) for a recent report; see also Savoy (1987).

Physiological studies

Syrkin *et al.* (1994a) investigated the responses of odd-

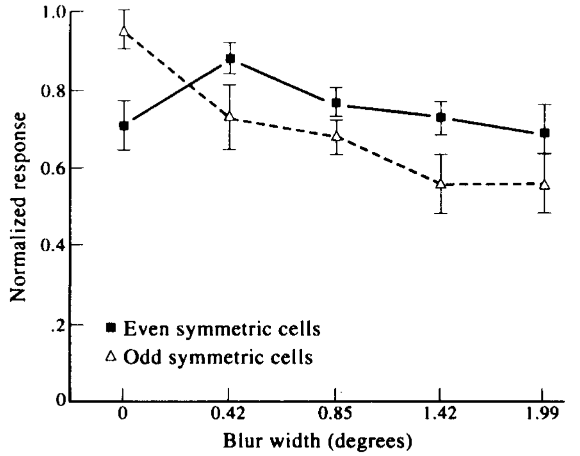

FIGURE 10. Responses of area 17 cells of the cat to luminance ramps of various widths from the study of Syrkin *et al.* (1994a). The even-symmetric responses should be compared to the experimental data shown in Fig. 5. Reprinted from Syrkin *et al.* (1994a) with permission.

and even-symmetric simple cells in cat area 17 to luminance distributions including steps and ramps of different widths (slopes). As expected, even-symmetric cells responded better to ramp stimuli, while odd-symmetric cells responded better to abrupt steps. It should be noted that the responses were not very localized in space, usually being stronger around the middle of the ramp (for even-symmetric cells) or at the location of the step (for odd-symmetric cells). Figure 10 shows the responses of cells to ramps of various widths. It is interesting to observe the resemblance between even-symmetric cell responses to ramp stimuli and the psychophysical sensitivity to Mach bands (see Fig. 5).

SUMMARY OF EXPERIMENTAL FINDINGS

Mach bands are stronger for ramps

The most conspicuous result of the recent psychophysical findings is that Mach bands are more pronounced for luminance ramps of intermediate width, being weak, or nonexistent, for a luminance step. The inconsistency of such a result and the lateral inhibition account has been repeatedly pointed out. At the same time, it is not entirely clear why Mach bands were observed in luminance steps in a few of the early studies. Two of the studies reporting Mach bands on luminance steps employed experimental techniques involving the temporal dynamics of brightness perception. Békésy (1968a) employed flicker photometry and Davidson (1966) employed brief presentation times. It is possible that in such experimental paradigms Mach bands are also strong for luminance steps. In fact, a prediction of a recent model is that Mach bands should occur at luminance steps for very brief presentation times as a result of the temporal dynamics of brightness perception. To anticipate, according to the model of Pessoa *et al.* (1995b), brightness is given by a diffusive filling-in process that takes time. For brief presentation times the (retinal) filtering overshoots and undershoots associated with a luminance step do not have the chance to be homogenized by filling-in, and Mach bands should be present (see Fig. 22). Overall, very few studies have explored the temporal dynamics of Mach bands and experiments are greatly needed here.

It should be noted also that even the sharpest luminance step is degraded because of imperfections of the eye. In fact, the blur is considerable and estimates of the "line spread function" of the human eye provide one such measure. For example, a vertical line of 1.6 arcsec, may span 10 arcmin or more on the retina (Krauskopf, 1962). Therefore, not only "perfect" physical steps do not produce perfect steps on the retina, but certain experimental paradigms may be more subject to smoothing in such a way that steps would produce narrow ramps. The possibility that these effects may be involved in the perception of Mach bands at abrupt luminance transitions needs to be carefully investigated.

Asymmetries of light and dark bands

There are several asymmetries between the appearance of light and dark Mach bands. Studies diverge as to whether light bands are stronger than dark bands or vice versa. Most of the early studies described light bands as more pronounced than dark bands—light bands are brighter than dark bands are darker—and thinner (Ratliff, 1965, p. 55). Several investigators have claimed that dark bands are stronger instead (Gur & Syrkin, 1993; Thomas, 1965; Ross *et al.*, 1989). The discrepancy may be related to the experimental procedures employed. Gur and Syrkin (1993), Thomas (1965) and Ross *et al.* (1989) all measured contrast threshold for seeing Mach bands. Most early experimental investigations employed brightness matching paradigms (supra-threshold). Further experiments are needed in order to clarify this issue. The dependence of light and dark bands on gradient slope also differs, with light bands being much more sensitive to changes (Ratliff, 1965; Fiorentini, 1972; but see Thomas, 1965). Several authors have suggested that while light and dark bands may be subserved by common mechanisms they may be mediated separately (Gur & Syrkin, 1993; Thomas, 1965; see also Ross *et al.*, 1989). One possibility is that light and dark bands are subserved by ON- and OFF-systems (Ratliff *et al.*, 1983).

Center-surround retinal mechanisms

Although it is clear that center-surround antagonistic interactions at the retina are insufficient to account for Mach bands, the results of Békésy (1968b) and Ross *et al.* (1981) strongly suggest that they are critical for the effect. These studies showed that the dark-adapted eye does not perceive Mach bands. Moreover, Békésy (1968b) showed that the appearance of light bands varies as a function of the exposure time after dark adaptation (i.e. light adaptation). The classic studies of Barlow *et al.* (1957) showed that the surround mechanism of cat retinal ganglion cells is less effective in the dark. Furthermore, light adaptation increases the prominence of the antagonistic surround relative to the center—decreasing the

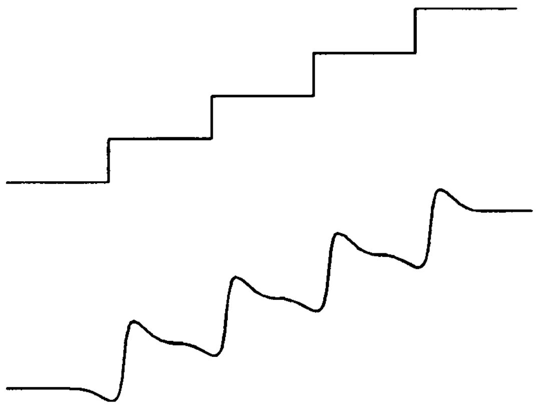

FIGURE 11. Chevreul illusion. Staircase luminance distribution (top) and schematic representation of the perceived brightness (bottom).

center-surround gain ratio from 3 to 1.2 with light adaptation (Enroth-Cugell & Lennie, 1975; Kaplan *et al.*, 1979). These physiological studies, taken together with the psychophysical studies of the perception of Mach bands under dark adaptation, strongly suggest that an intact center-surround retinal structure is necessary for the generation of the bands.

Synergy between theory and experimentation

The recent findings also reveal the synergy between theory and experimentation. Once theoretical frameworks were able to emerge that provided alternatives to the lateral inhibition or contrast sensitivity approach to vision, researchers were able to formulate new experimental paradigms that explored new aspects of the appearance of Mach bands and their relationship to other early vision processes. The studies of Morrone, Burr and colleagues on the importance of phase information for visual processing illustrate this point well.

The recent physiological studies of Syrkin *et al.* (1994a,b) demonstrate the potential of integrating physiological, psychophysical and computational approaches, as was done in the early studies of Mach bands, of which Ratliff's work is perhaps the best example (Ratliff, 1965). However, while such avenues for research are very promising, their interpretation requires care. In the context of Syrkin and colleagues' (1994a) work, while it is interesting to note the resemblance between cell responses to ramp stimuli and the psychophysical sensitivity to Mach bands compare Figs 5 and 10), it is premature to conclude that "simple cells may be the physiological basis for the Mach band phenomenon" (Syrkin *et al.*, 1994, p. 326). First, more detailed analysis of the dependency of cell response and spatial frequency selectivity is required. Second, care must be taken when ascribing the explanation of a perceptual effect to the responses of *single* cells (see Teller, 1980, 1984). Finally, to the extent that odd- and even-symmetrical cells deserve their names at all, they will, by definition, respond more strongly to edges and ramps, respectively. The observation that actual simple cells behave in this way is important, but hardly suffices to indicate that these constitute the basis for the perception of Mach bands.

OTHER BRIGHTNESS EFFECTS

An effect that is often discussed in the context of Mach bands is the Chevreul illusion, named after the French chemist Michel-Eugène Chevreul (1839). Figure 11 illustrates both the luminance distribution and a schematic representation of the perceived brightness with its "scallopy" or "fluted" appearance. Several researchers have described the Chevreul illusion as essentially the same as Mach bands (e.g. Hurvich, 1981, p. 164); this is also common in introductory perception textbooks (e.g. Goldstein, 1989). While the two illusions are superficially similar, it is important to distinguish between them, especially given the large body of evidence showing that luminance steps do not produce Mach bands under most conditions, if at all. Ross *et al.* (1981) investigated both the Chevreul illusion and Mach bands and suggest that different physiological mechanisms may underlie their perception since the Chevreul illusion is (a) unaffected by dark adaptation; (b) is present both at low and high spatial frequencies (up to at least 15 panels/deg); and (c) the scalloping alternates with the veridical appearance (i.e. the percept in Fig. 11 alternates with the percept of an undistorted staircase). An important property of stimuli that produce the Chevreul illusion is that they have at least *three* panels (Békésy, 1968b). One step is *not* sufficient to generate the effect, but at least two are necessary (aside from the "outer border edges"). This often forgotten requirement demonstrates that any links between Mach bands and the Chevreul illusion require careful investigation.

Mach bands have often been linked to *brightness contrast* effects such as found in introductory perception textbooks where a mid-gray square is displayed on different intensity backgrounds. One of the important conclusions of the Ratliff *et al.* (1983) study is that these contrast phenomena are not Mach bands. They point out that if the border contrast at a step were itself a Mach band then a nearby step (of the proper polarity) should enhance rather than attenuate (as they found) the adjacent Mach band. Note that their triangular stimulus [see Fig. 6(D)] had a clear enhancing effect on the adjacent Mach band. At intermediate distances, a triangular stimulus produces a band twice the usual width, as the bands of the triangular stimulus and the ramp "fuse".

van den Brink & Keemink (1976) have investigated the perception of luminance sawtooth distributions and proposed that they are subserved by a different set of mechanisms than Mach bands. They were interested in investigating whether Mach bands and "edge effects" such as produced by Craik–O'Brien–Cornsweet cusps are produced by the same mechanisms. Their main finding was that the perception of certain saw-tooth patterns depended on interpretation (being seen as two- or three-dimensional), suggesting to them that these patterns are subject to more "central" processes, as opposed to being due to lateral inhibition mechanisms at the retina as was suggested by some for Mach bands at the time. Given that current models predict that Mach bands occur no sooner than area V1 where simple and complex cells are found, and the recent results on the influence of factors such as shape, transparency and shadows on brightness perception (Knill & Kersten, 1991; Adelson, 1993; Pessoa *et al.*, 1995a; Arend *et al.*, 1995), it would be instructive to investigate whether Mach bands can be affected by these or other "high-level" effects. Hodgkinson and O'Shea (1994) showed that Mach bands can be interpreted as specular highlights in computer graphics displays (an effect that can be observed by displaying a trapezoidal wave on a CRT) and studied their effect on perceived glossiness.

RECENT THEORIES

Since Mach (1865) first reported them, Mach bands have attracted a large number of investigators who have attempted to explain the phenomenon. The theories reviewed below vary in complexity. Most were proposed as general schemes for understanding early visual processing, and have addressed the issue of the appearance of Mach bands to different extents. Some are proposals specific to Mach bands. While all proposals greatly differ from one another in detail, they can be

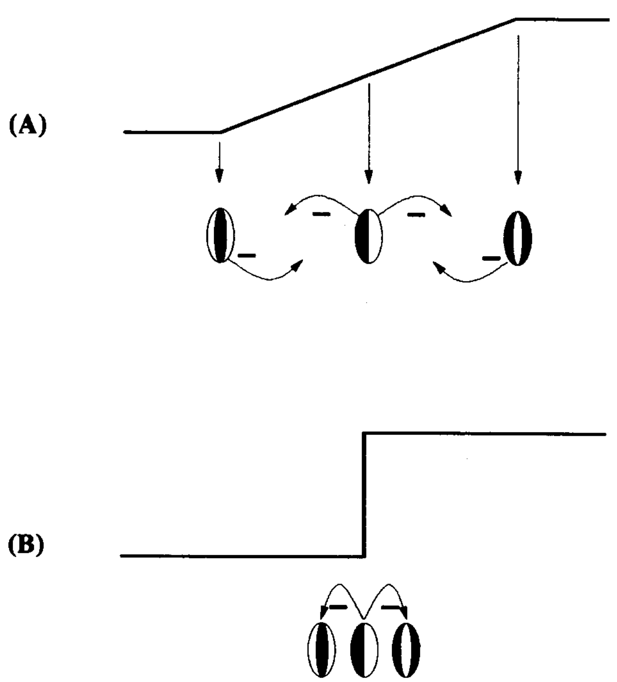

FIGURE 12. Scheme proposed by Tolhurst (1972) to account for Mach bands. (A) Optimal edge and bar detectors respond maximally at diferent positions along the ramp (see arrows); operators not drawn to scale. If maximal edge and bar responses are far enough from each other, as in a ramp, the bar detectors are not inhibited and are able to signal Mach bands. (B) In a luminance step, edge detectors inhibit nearby bar detectors. No Mach bands are predicted.

grouped in three classes: (a) feature-based; (b) rule-based; and (c) filling-in. Feature-based theories postulate that edges and lines are basic primitives of early vision. Specific proposals differ in the ways primitives are detected and how the detection operators—i.e. even- and odd-symmetric mechanisms—interact when more than one type is used (competition or cooperation). Rule-based theories may also employ primitive features, but what distinguishes them is a stage of brightness description by the application of a fixed set of rules interpreting what the convolution responses map to. Filling-in theories propose that the spreading of neural activity within filling-in compartments produces a *spatial* response profile that resembles the percept. A major conceptual difference exists between feature-based and ruled-based theories on the one hand, and filling-in theories on the other. According to the former, one of the main tasks of the visual system is to detect salient features (e.g. lines and edges). Most of the "detail" in scenes is ignored. The latter theories attempt to build representations that preserve the geometric structure of percepts. These ideas will be expanded in the next section.

Seven recent models have attempted to account for Mach bands. The first four are feature-based, the next two are rule-based and the last is a filling-in proposal. All models are multi-scale theories of vision. The proposals discussed are:

- Inhibition of edge and bar detectors (Tolhurst, 1972).
- Local energy (Morrone & Burr, 1988).
- Multi-channel (Fiorentini *et al.*, 1990).
- Cell assembly (du Buf, 1994).
- MIRAGE (Watt & Morgan, 1985).
- MIDAAS (Kingdom & Moulden, 1992).
- Filling-in (Pessoa *et al.*, 1995b).

The following discussion will concentrate on the different ways in which these models account for Mach bands. Although the application of the models to other phenomena is beyond the scope of the present article, overall it is important to consider how they address different but related phenomena. In other words, the power of a specific approach stems from its ability to show how related phenomena originate from a common set of mechanisms or processes. For example, though distinct, Mach bands and the Chevreul illusion are clearly related effects. Thus, ideally, theories should be able to handle both of them.

A striking feature of the recent formalisms is that *all* provide explicit explanations for the lack of Mach bands on luminance steps, and special attention will be paid to how this is accomplished. A central theme of the discussion below will concern the nature of the "decoding rules" or *linking propositions* (Teller, 1980, 1984) employed, implicitly or explicitly, by each model. These propositions, or hypotheses, are directly related to key issues of current visual science, such as the use of multiple spatial scales and the types of visual "features" (e.g. lines and edges).

Feature-based theories

Inhibition of edge and bar detectors. Tolhurst (1972) showed that adaptation to a pattern of, say, left–right symmetry (e.g. a luminance step) produced greater threshold elevation for test patterns of the same polarity than to patterns of the opposite polarity. This was taken as evidence for the existence of odd-symmetric operators—"edge" detectors—in the visual system. Tolhurst also suggested that spatially limited mutual inhibition between edge and bar (even-symmetric) detectors could be used to explain several brightness illusions, including Mach bands. Consider a luminance ramp that elicits Mach bands. The optimal edge detector response is on the middle of the ramp, and the optimal bar detector responses are at the inflection points. As long as the bar detectors are far enough from the edge detectors so as to not be inhibited by them, they will signal the presence of bars, i.e. light and dark Mach bands [Fig. 12(A)]. Tolhurst's proposal can also account for why Mach bands are not seen on a step. For such luminance distribution, both edge and bar detectors located at or near the step are activated. Since the edge detectors will be maximally activated, they can suppress the smaller activity of the bar detectors activated by the step. No Mach bands are seen [Fig. 12(B)].

Ratliff (1984) set out to test Tolhurst's scheme by positioning a biphasic bar in the middle of a narrow luminance ramp (see Fig. 6 for a cross-section of a biphasic bar). According to him, the variable contrast biphasic bar would provide independent control of the strength of the two competing mechanisms. High-contrast biphasic bars would produce strong responses from odd-symmetric operators in the middle of the ramp and effective attenuation of the bands. For low-contrast biphasic bars, the weak inhibition from the bars would not be able to remove the bands. As mentioned above, his finding was that as the contrast of the biphasic bar was increased light and dark band width decreased. The results were taken as evidence that some version of Tolhurst's scheme was correct.

The Tolhurst–Ratliff scheme is attractive due to its simplicity. It relies, however, on interactions between multiple spatial scales. Only coarse scale odd-symmetric cells respond strongly for the ramp center and can signal an edge. At the same time, small-scale even-symmetric cells are required for responding at the inflection points and signaling bars. There are several ways to specify Tolhurst's scheme as a functioning model, but all need to prevent "spurious" responses from occurring so that even- and odd-symmetric mechanisms do not signal extra features at incorrect locations.

More serious objections to the Tolhurst–Ratliff proposal originate from considering the Ratliff *et al.* (1983) data more closely. The proposal is not consistent with the fact that both regular bars [Fig. 6(A)–(B)] and biphasic bars [Fig. 6(C)] attenuate Mach bands to similar extents. While biphasic bars more strongly activate odd-symmetric, or edge, operators, regular bars more strongly activate even-symmetric, or bar, operators. Thus, regular bars should not attenuate Mach bands. The Tolhurst–Ratliff proposal also encounters problems explaining why the width of the adjacent stimulus is not important. Narrow bars (e.g. 2.5 arcmin) strongly activate only even-symmetric mechanisms, while wider ones (e.g. 100 arcmin) produce stronger responses from high spatial frequency odd-symmetric cells (locally the adjacent stimulus will be an edge). Finally, Craik–O'Brien half-cusps attenuate Mach bands to the same extent that adjacent bars do (Pessoa, 1996). Such stimuli also activate bar detectors more strongly than edge detectors and therefore, according to the Tolhurst–Platliff scheme, should not attenuate Mach bands.

Local energy. Although models of early visual processing differ widely, they share the property that incoming inputs are first filtered by even-symmetric receptive field-like operators; a few use odd-symmetric operators instead (e.g. Canny, 1986). Morrone and Burr (1988) proposed that by combining the output of both even- and odd-symmetric operators, it is possible to account for a large body of psychophysical data. Their model employs two sets of matched operators and uses them to obtain a "local energy" measure at every location of the visual scene. Local energy is defined as the

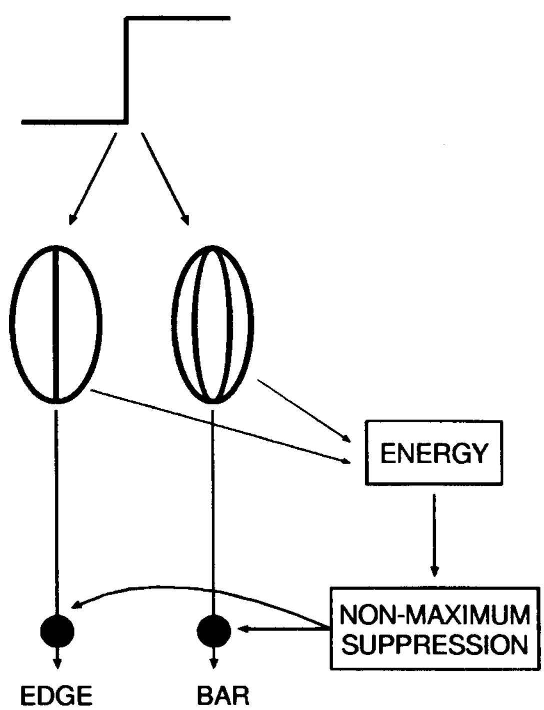

FIGURE 13. Local energy model of Morrone and Burr (1988). Local energy is computed at every position. The positions at which it peaks mark visually salient features (lines and edges). At these positions, the responses of even- and odd-symmetric operators indicate the type of feature associated with the peak; even-symmetric responses signal the presence of a line and odd-symmetric responses signal the presence of an edge. The location of the sharp luminance transition is thus marked "edge". All other positions (not shown) do not convey information about visual features since they are suppressed (filled circles).

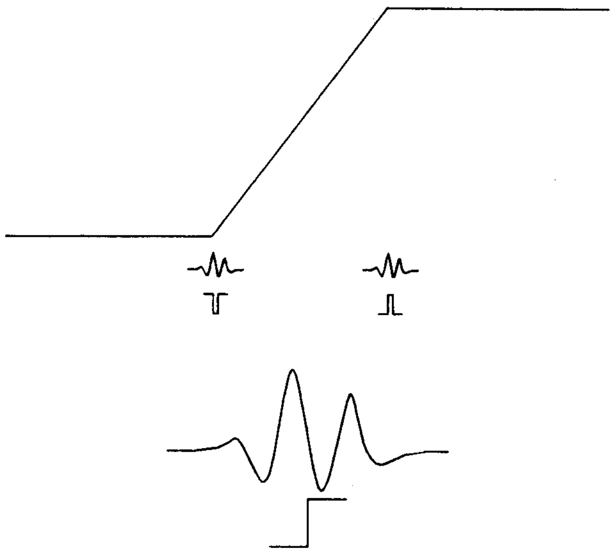

FIGURE 14. Multi-channel explanation of Mach bands with small- and large-scale channels. The small-scale channel signals light and dark bands at the inflection points, and the large-scale channel signals a dark-to-light transition in the middle of the ramp.

square-root of the sum of the squares of the filter responses and is used to indicate the positions of "features". Figure 13 illustrates the main computations of the Local energy model. (1) The stimulus is filtered by even- and odd-symmetric operators (possibly in multiple scales). (2) local energy is computed at every position. (3) Determination of local energy peaks by non-maximum suppression. The locations of local energy peaks—and only these—indicate the positions of salient features, such as lines and edges. The nature of the feature is determined by the outputs of the even- and odd-symmetric operators determined in the first step. If the peak of local energy coincides with the peak of an even-symmetric filter, the stimulus is a line (or bar). If it coincides with the peak of an odd-symmetric filter, the stimulus is an edge. An important property of the local energy model is that it is capable of signaling "mixed" features, such as edge–bar combinations. In other words, if at a given energy peak both even- and odd-symmetric operators have non-zero responses, the model signals the existence of a feature having properties of both lines and edges.

The local energy model predicts the presence of Mach bands for several waveform types. At the position where a luminance ramp meets a plateau, a peak in local energy occurs. Since the activity at such positions is greater for even-symmetric operators, the feature is signaled as a line, or band. For a luminance step distribution, no band will be signaled since the peak of local energy at the step is associated with odd-symmetric responses—the signal for an edge. Ross *et al.* (1989) have shown excellent data fits, demonstrating that the local energy model can quantitatively match several results on Mach bands. Moreover, Morrone, Burr and colleagues have shown how the model can quantitatively address several other effects (Morrone & Burr, 1988), including a new (modified) Chevreul illusion (Morrone *et al.*, 1994).

The local energy model proposal is similar to that of Tolhurst (1972) in that both schemes employ pairs of orthogonal operators. The most important difference is that while Tolhurst invokes mutual inhibition between the two types of operators (in order to eliminate bar responses at a luminance edge), Morrone and Burr suggest that they cooperate in the computation of local energy—an operation which indicates visually salient features.

Physical contrast determines the appearance of many stimuli. This is a problem for the local energy model since the positions of the peaks in local energy that constitute the output of the model and signal important features are invariant with regard to input stimulus amplitude (see also Kingdom & Moulden, 1992). Thus the model cannot, without modifications, account for, say, why the missing fundamental stimulus is perceived differently as a function of contrast; as a square-wave for low contrast and with the "veridical" cusps for higher contrasts. The same problem is encountered when processing low- and high-contrast sinusoidal waves—the latter are perceived in a deformed way while the former in a more veridical form. Perhaps by applying an initial compressive non-linearity before the computation of local energy, some of these problems may be overcome. See Georgeson (1994) for an evaluation of the local energy model for low-frequency brightness patterns.

Multiple channels. As discussed, the lateral inhibition model of Mach bands is incorrect since it predicts that the effect should be strongest at a luminànce step. Fiorentini *et al.* (1990) described how a single-scale model (see Fig. 2) can be extended to multiple scales so as to account for this discrepancy. They propose the use of two channels, one selective for high spatial frequencies (small-scale channel) and one selective for low spatial frequencies (large-scale channel). When applied to a luminance ramp, the large-scale channel responds to the ramp just as it does to a luminance edge (Fig. 14). This response can be associated with a brightness change from dark to light. The small-scale channel is insensitive to the ramp, responding only to the two inflection points in the stimulus. Such responses are similar to the ones a small-scale channel would generate in response to dark and light bars alone and can be said to signal the presence of dark and light bars at the extremes of the ramp. Finally, the overall percept is considered to be the composite of the large- and small-scale responses, which can be interpreted as a brightness step with flanking dark and bright bars. The bars correspond, of course, to Mach bands.

When a luminance step is processed by these two channels, they will both respond at the same location. The individual responses will be interpreted as signaling an edge, and so will the composite response. No flanking bands are signaled.

The multi-channel proposal employs a single filter

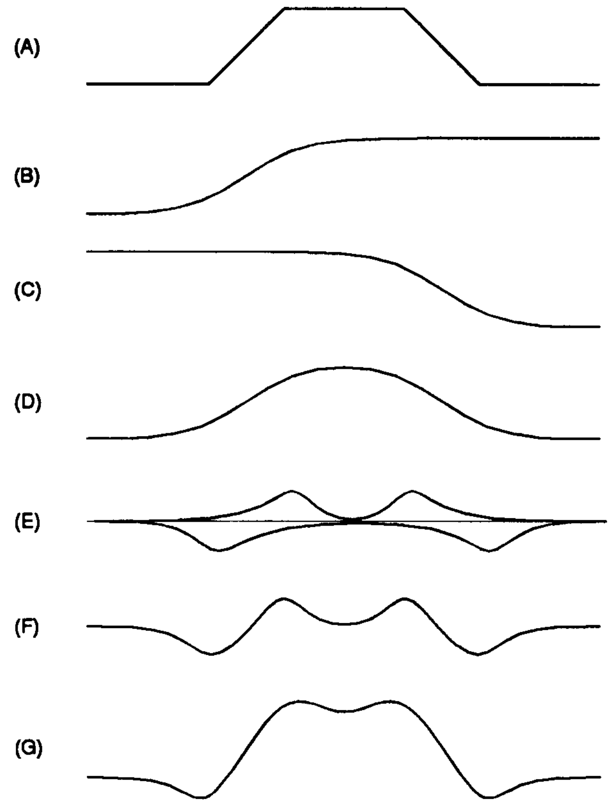

FIGURE 15. Illustration of the syntactical reconstruction process of Mach bands by the Cell assembly model. (A) Trapezoidal luminance. Error function-shaped light (B) and dark (C) edges. (D) Sum of (B) and (C). (E) Gaussian lines associated with the inflection points. (F) Sum of Gaussian lines. (G) Final combination corresponding to the sum of (D) and (F). Adapted from du Buf (1994) with permission.

type. "Bar" responses are assumed whenever any stimulus locally produces a response that is similar to the one elicited by a luminance bar itself. "Edge" responses occur whenever a stimulus locally produces a response that is similar to the one elicited by a luminance step itself. In order to be operational, however, the scheme needs to formalize the notion of similarity. The rule-based models MIRAGE and MIDAAS that are discussed below can be viewed as examples of proposals to formalize similarity through the use of explicit decoding rules employing the pattern of zero-crossings (Marr & Hildreth, 1980) produced by filtering.

Cell assembly. du Buf (1993) studied the responses of "complex" simple cells to lines and edges. His simple cells are operators that can be understood as abstractions of two simple cells, both centered at the same location, but in quadrature (i.e. having a phase difference of $\pi/2$). du Buf (1994) extended this analysis to investigate how such operators react to luminance ramps. The main computational stages of the cell assembly model are: (1) The stimulus is filtered by "complex" simple cells at several spatial scales. (2) These signals are employed in a process of visual reconstruction to predict visual appearance.

The question du Buf (1994, p. 454) poses himself is the following: "when there are event detectors that act on the basis of the simple cell responses ... what information would they use and how would the information at different scales be combined?" du Buf proposes a "syntactical reconstruction principle" whereby the initial filtering responses are interpreted in terms of *Gaussian lines* and *error-function-shaped edges.* In other words, the basic reconstruction vocabulary is composed of lines and edges. For the processing of a trapezoidal wave, Gaussian lines correspond to blurred versions of the filtering overshoots and undershoots at the inflection points. Error-function-shaped edges correspond to blurred or smoothed edges associated with the luminance ramps. The final reconstructed waveform is a trapezoidal waveform with overshoots and undershoots. Therefore, Mach bands are the result of how the reconstruction process recovers lines and edges (Fig. 15). The reconstruction process does not generate undershoots and overshoots to abrupt luminance transitions, correctly predicting that no Mach bands are seen. This occurs since only an error-function-shaped edge is used in the reconstruction of a luminance step.

du Buf (1994) also shows simulation results illustrating the attenuation of Mach bands in the case of a bar located in the middle of the ramp, as observed experimentally (Ratliff, 1984). Although the model results are consistent with the data, the model needs to be more completely specified in order to be properly evaluated (but see du Buf and Fischer, 1995).

Rule-based theories

MIRAGE. The MIRAGE model of Watt and Morgan (1985) was proposed to provide a general symbolic description of local luminance changes in visual stimuli. In effect it can be understood as a development of the framework originally proposed in Marr's (1982) concept of the primal sketch; see Watt (1988). MIRAGE transforms a visual scene into a spatially ordered list of discrete (symbolic) primitives and can be described in five computational stages. (1) The stimulus is first filtered by even-symmetric operators at several spatial scales. (2) The responses are split into their positive and negative portions. (3) All positive signals are added together across scales (T^+); the same is done for negative signals (T^-). 4) The resultant signals are then used to generate a list of primitives. There are two types of primitives, a *zero-bounded response* and a *region of inactivity*. (5) Finally, three fixed rules are used in order to interpret the sequence of primitives: the *null rule* corresponding to a luminance plateau, the *edge rule*, and the *bar rule.* This last stage allows inferences about luminance variations or brightness changes in the scene.

The names of the three rules indicate that MIRAGE is interested in determining the main features present in images (i.e. lines and edges). MIRAGE postulates that this task can be accomplished by interpreting the distribution of zero-bounded responses and regions of inactivity (the two primitives). A zero-bounded response corresponds to a peak of the filtering response bounded

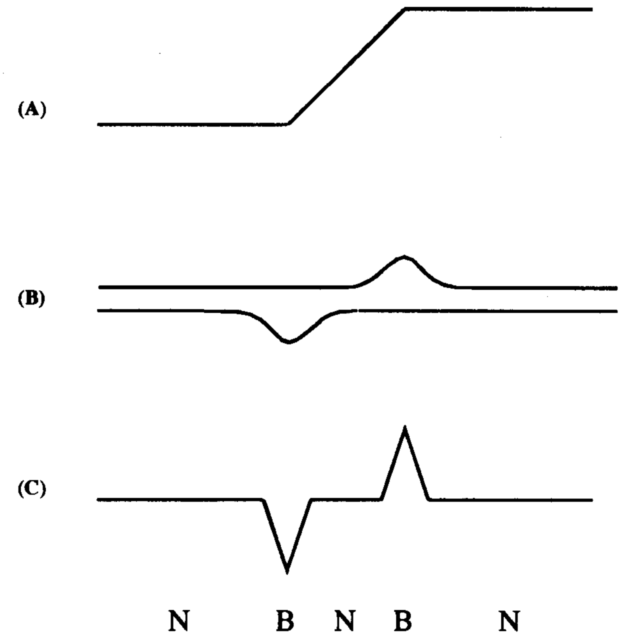

FIGURE 16. MIRAGE and the perception of Mach bands. (A) Ramp luminance distribution. (B) Positive and negative summed across scales signals (T^+ and T^-). These signals correspond to overshoots and undershoots from the initial filtering that have been separated. (C) Rules triggered at given spatial locations (N: null rule; B: bar rule). Note that the bar rule was triggered twice due to the zero-bounded responses originating from the ramp inflection points. The triggering of the bar rule indicates Mach bands. Adapted from Watt and Morgan (1985) with permission.

by two outer zero-crossings (Marr & Hildreth, 1980). Regions of inactivity are also explicitly encoded (see Watt & Morgan, 1983). Edges are, then, indicated by a zero-bounded response with a region of inactivity on only one side (the edge rule). Bars are indicated by a zero-bounded response with a region of inactivity on both or neither side (the bar rule).

MIRAGE has attempted to explain brightness percepts such as the Chevreul illusion and Mach bands, among other phenomena. Figure 16 shows how the model accounts for Mach bands and illustrates the use of its rules. The activity associated with the inflection points of the ramp produces zero-bounded responses (stage 4) which are then interpreted by the bar rule (stage 5). Therefore, at the positions where Mach bands are generally perceived, MIRAGE signals "bars" or bands.* In the case of a luminance step (or a ramp of limited width), MIRAGE will trigger the "edge" rule at the position of the step, thereby correctly predicting that Mach bands disappear at abrupt luminance transitions.

MIRAGE predicts that the critical width for Mach bands should also apply for the Chevreul illusion (Watt & Morgan, 1985, p. 1666). Ross *et al.* (1981) reported that the Chevreul illusion occurred for high spatial frequencies up to at least 15 panels/deg, indicating a minimal plateau width of 4 arcmin or less. For Mach bands, the study of Ross *et al.* (1981) reported a minimal ramp width of 7.5 arcmin; a subsequent study by Ross *et al.* (1989) reported a minimal width of 4 arcmin. Further quantitative measurements are needed in order to determine whether the Chevreul illusion can be elicited for narrower plateaus, and thereby assess MIRAGE's prediction.

MIRAGE has not been used to provide quantitative predictions on Mach bands. In this context, Ross *et al.* (1989) have pointed out that it cannot account for the close dependence of Mach bands on spatial frequency. According to their simulations, MIRAGE does not account for the fact that as ramps decrease in width, Mach band strength decreases. Instead, MIRAGE predicts just the opposite (before Mach bands disappear altogether).

MIDAAS. Kingdom and Moulden (1992) have proposed a multi-scale model of brightness perception called MIDAAS which has addressed a large set of brightness stimuli. MIDAAS has five processing stages. (1) Light adaptation is performed by a mechanism of gain control. (2) The stimulus is filtered at multiple spatial scales. (3) The outputs are thresholded and subject to a power-law transformation for each scale. (4) The filtered responses (stages 1–3) are used to generate symbolic descriptions of brightness changes for each spatial scale separately. More precisely, after the input is convolved, *interpretation rules* are used to determine the brightness prediction associated with each spatial scale. Rules specify how filtered responses are interpreted in terms of single-scale brightness predictions according to properties of the filtered responses, i.e. the pattern of zero-crossings. (5) Stage five combines the outputs of all scales by averaging the reconstructed profiles. This averaged across-scales output corresponds to the final predicted percept. Figure 17 illustrates the behavior of the interpretation rules used by MIDAAS showing how filter responses are interpreted as indicating the presence of an edge (A), and a bar [(B) and (C)].

MIDAAS can account for both triangle and trapezoidal Mach bands. This is obtained by employing interpretation rules that allow the model to preserve overshoots and undershoots of the convolved responses. At positive and negative inflection points of a trapezoidal wave responses are produced indicating bars, or bands (for several scales); such as illustrated in Fig. 17(C) for a triangle luminance input. The combination of these responses with one originating from the lowest spatial frequency that registers the overall trapezoidal modulation, correctly predicts the appearance of a trapezoidal wave. According to Kingdom and Moulden (1992), MIDAAS can account for the effect of spatial frequency on Mach band appearance (although no simulations are shown), and correctly predicts the absence of Mach bands for a square-wave since no "bar responses" are produced [see

*In generating Fig. 16, it was assumed that the input was initially filtered with ON-center OFF-surround even-symmetric operators. Watt and Morgan (1985) use, instead, OFF-center ON-surround operators.

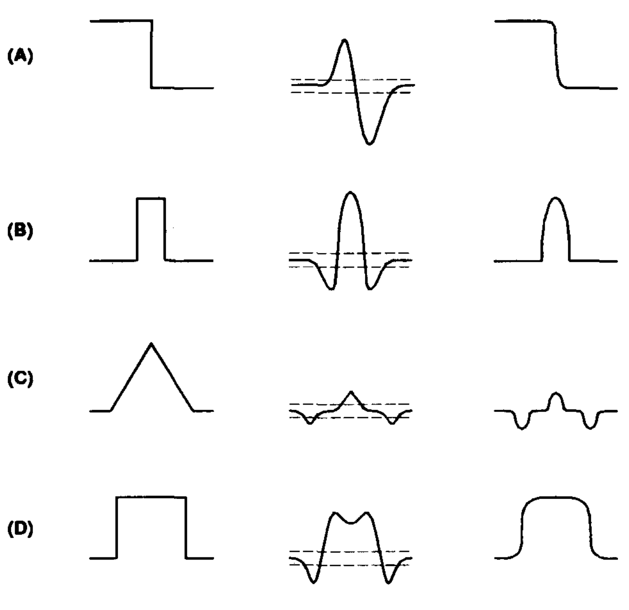

FIGURE 17. Brightness predictions generated by MIDAAS. After the initial processing of the input distributions (left), rules specify how filtered responses (middle) are interpreted in terms of single-scale brightness predictions (right) according to the pattern of zero-crossings and amount of contrast. Adapted from Kingdom and Moulden (1992) with permission.

Fig. 17(D)]. Interestingly, MIDAAS can correctly predict the attenuation of Mach bands when bars are superimposed on the ramps (Ratliff, 1984). Kingdom and Moulden (1992) conclude that no mutual inhibition between odd- and even-symmetric operators is required to account for this effect, as postulated by Ratliff (1984); see below.

As is the case for other rule-based theories, the power of MIDAAS stems directly from its set of interpretation rules. Even more for MIDAAS, as its rules are tailored to brightness perception, and are not "general rules" (such as in MIRAGE).

Filling-in theories

Filling-in models propose that spreading of neural activity within filling-in compartments produces a response profile that spatially resembles the percept (Fry, 1948; Walls, 1954; Gerrits & Vendrik, 1970; Hamada, 1984; Cohen & Grossberg, 1984; Grossberg & Todorović, 1988). Traditionally it has been assumed that filling-in models cannot account for Mach bands (e.g. Kingdom & Moulden, 1992, p. 1579; Blomnaert & Martens, 1990, p. 27). One reason is that filling-in as specified by boundary-gated diffusion has been *functionally* interpreted to mean "averaging between edges"—i.e. the final equilibrated output is *constant* within a region. This is certainly a *possible* outcome produced by filling-in models. However, the emphasis of such models is in the role of contours, or boundaries, in determining visual surface perception. Whether "brightness" is completely uniform or not within regions is not the central issue.

The remarks on filling-in and Mach bands above are interesting in view of the fact that historically filling-in mechanisms were suggested, in part, in order to account for the lack of Mach bands on sharp edges.† For example, Fry (1948) introduced a "frequency-equalizing" mechanism having as one of its functions the reduction of brightness gradients adjacent to sharp edges.

Contrast- and luminance-driven brightness perception. Pessoa *et al.* (1995b) presented a filling-in model of brightness perception based on previous work by Grossberg and colleagues on the Boundary Contour System and Feature Contour System (Cohen & Grossberg, 1984; Grossberg & Mingolla, 1985a, b; Grossberg, 1987; Grossberg & Todorović, 1988). The model accounts for Mach bands and other stimuli by employing boundary computations that are sensitive to luminance steps as well as luminance gradients. Following the proposal of Neumann, (1993, 1996) two processing streams were employed, a contrast-driven channel and a luminance-driven channel. There are four main computational stages. (1) The input stimulus is decomposed into separate contrast-driven and luminance-driven representations. (2) Contrast-driven signals from ON/OFF filtering are employed to produce boundaries. (3) Contrast-driven signals are also used as feature signals that undergo boundary-regulated diffusion. (4) Contrast-driven and luminance-driven signals are recombined providing the final model output.

When processing a luminance ramp, spatially extended boundary signals of sufficient amplitude—called *boundary webs* by Grossberg and Mingolla (1987)—are generated which are able to block, or trap, the diffusion of the overshoots and undershoots present in the ON/OFF filtering signals — which in this context are called feature signals as they directly contribute to brightness. Thus the overshoots and undershoots are preserved in the final equilibrated filling-in, producing Mach bands in the brightness output (see Fig. 18). Note that filling-in contributes *only* to the production of the light and dark bands and that the ramp modulation originates from the luminance-driven channel. For a luminance step no Mach bands are generated, since boundary computations produce a localized signal (at the edge) that allows the diffusion of the overshoot and undershoot, thereby making uniform the brightness distribution around the edge (see Fig. 19). For the luminance step, a localized boundary signal is generated due to the abrupt luminance transition.

The filling-in model presented by Pessoa *et al.* (1995b) differs from other proposals by Grossberg and colleagues (e.g. Grossberg & Todorović, 1988) by employing

†Several researchers have discussed the fact that most brightness contrast effects are rather uniform over large areas and proposed underlying two-stage processes —i.e. lateral inhibition followed by some smoothing operation. See Ratliff and Sirovich (1978) for a discussion of this theme in the context of so-called isomorphistic and non-isomorphistic neural representations.

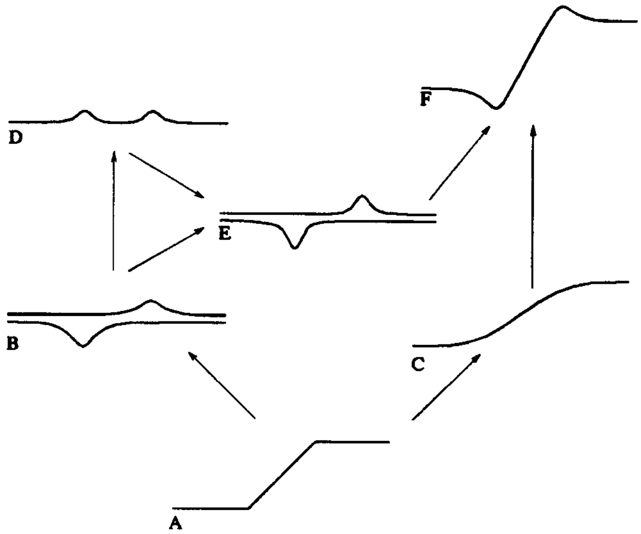

FIGURE 18. Filling-in model with contrast- and luminance-driven channels processing a luminance ramp. (A) Luminance ramp. (B) Contrast-driven signals from ON (top) and OFF filtering (bottom) showing overshoots and undershoots. (C) Luminance-driven "low-pass" signal. (D) Boundary signals extend over the region of filtering activity. (E) ON (top) and OFF (bottom) (equilibrated) filling-in; ON/OFF filtering responses are largely blocked. (F) Final brightness. Mach bands are generated.

explicit representations of contrast-driven and luminance-driven information and by employing boundary computations sensitive to both sharp and smooth luminance transitions. While the Grossberg and Todorović (1988) implementation produced Mach band-like effects for some parameter choices, it did not account for the fact that Mach bands are stronger for ramps and are weak, or nonexistent, in luminance steps. This is treated adequately in the Pessoa *et al.* (1995b) scheme which can also quantitatively fit some of the results of Ross *et al.* (1989).

EVALUATION AND COMPARISON OF MACH BAND MODELS

Summary of theories

All six models reviewed by Ratliff (1965) involved lateral inhibition and could be essentially understood as a single proposal. All of them failed to indicate that abrupt luminance transitions do not produce Mach bands. On the other hand, all recent proposals reviewed above correctly predict that this does not occur since all of them supplement lateral inhibition, or filtering, by either more sophisticated filtering schemes, or other mechanisms (e.g. rules). This obviously reflects the current move towards more sophisticated, multi-level vision theories. Figure 20 summarizes the models reviewed.

Representation

The central assumption of most models reviewed is that one of the major tasks of the visual system is to quickly extract the most salient information from an image. In the process, detail, such as the gradual variation of luminance, is lost. This philosophy underlies the choice of lines and edges as the basic *primitives* of early vision and can be traced back to Marr's proposal of a primal sketch as an early symbolic form of representation for scenes (Marr, 1976, 1982).

Although the models reviewed have different target domains, in general, the use of only lines and edges as the form of early representation is insufficient. Models of early visual processing must go beyond the tagging of important luminance changes if they are to be used as the basis for mid-level vision processes such as image segmentation and the representation of shapes. Illusory contours (Kanizsa, 1955, 1979) provide a striking example of the existence of contours (sometimes accompanied by brightness changes) where no physical luminance changes occur. It is interesting to note that Marr was concerned with both intensity changes and their geometrical organization in his (full) primal sketch and employed a rich set of primitives at this level: zero-crossings, blobs, terminations and discontinuities, edge segments, virtual lines, groups, curvilinear organization and boundaries (Marr, 1982, p. 37). In this context, Watt (1994) has proposed recently that the initial stages of human vision are more concerned with the whole area of the image than with the extraction of primitive features such as edges. Watt proposes the use of coarser spatial scales than those that are suitable for producing edge maps. The responses from such filters are then used as the basis for grouping operations (Grossberg & Mingolla, 1985a, b; Field *et al.*, 1993).

The impoverished representation adopted by recent models has led several of them to predict that Mach bands occur on luminance ramps but to disregard the fact that a gradient of brightness is also perceived. For example, MIRAGE codes the ramp as a region of inactivity. The

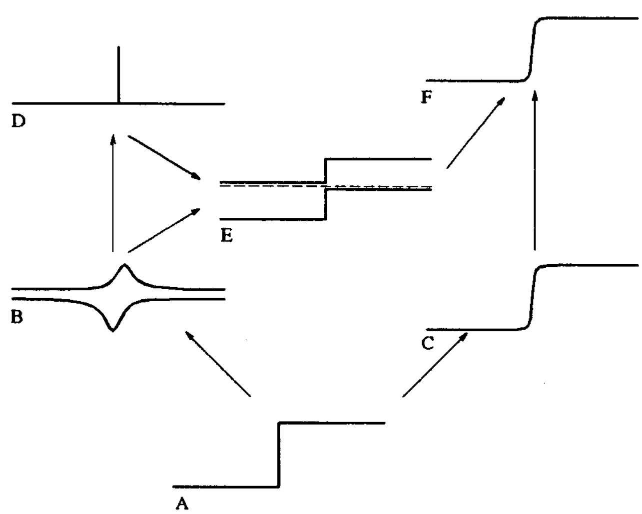

FIGURE 19. Filling-in model applied to a luminance step. The same stages as in Fig. 18 are shown. The ON (top) and OFF (bottom) adjacency of filtering (B) leads to the formation of localized boundaries. Filling-in (E) in the ON (top) and OFF (bottom) channels can proceed freely. No Mach bands are produced (F).

Model	Class	Mechanism	Multiple Scales	Data fits
Edge–Bar inhibition	feature–based	Bar response at inflections too far to be inhibited by edge response on the ramp	necessary	qualitative
MIRAGE	rule–based	Bar rule triggered at ramp inflections	not necessary	qualitative
Local energy	feature–based	Local enery peaks associated with even–symmetric operators	not necessary	quantitative
Multi–channel	feature–based	Small–scale channel signals bands and large–scale channel signals step	necessary	qualitative
MIDAAS	rule–based	Symbolic rules preserve filtering overshoot and undershoot	necessary	qualitative
Cell assembly	feature–based	Line and edge reconstruction	necessary	qualitative
Filling–in	filling–in	Filling–in of filtering overshoots and undershoots trapped by boundaries	not necessary	quantitative

FIGURE 20. Summary of the models reviewed (in chronological order). The column "Mechanism" summarizes how the models explain Mach bands. Also indicated are whether such accounts require multiple scales and the type of data fits published.

Tolhurst and the Fiorentini *et al.* schemes predict that instead of a ramp, a brightness step is seen at the middle of the ramp. Brightness gradients are ubiquitous in natural scenes and need to be accounted for by theories that model brightness data. For example, Arend *et al.* (1995) and Pessoa *et al.* (1996) have investigated the perception of lightness in three-dimensional ellipsoids illuminated from the side and shown an improvement in lightness constancy compared to those obtained with flat rectangular shapes under similar illumination conditions. In other words, not only gradual luminance variations are not lost, but they are probably treated differently depending on other visual cues, such as shape. It is interesting to note that Bergström (1994) argues that seeing the illumination is a condition for proper surface lightness (and color) perception, not an alternative to it (see also Gilchrist, 1994), in sharp contrast to Land and McCann's (1971) influential proposal that lightness constancy is the result of the low sensitivity of the visual system to smooth luminance gradients. Finally, smooth luminance gradients are required for the proper perception of three-dimensional shape and are employed by "shape-from-shading" algorithms (e.g. Bergström, 1977; Horn & Brooks, 1989).

Interpretation rules

A critical assumption of rule-based models, such as MIDAAS and MIRAGE, is the set of interpretation rules used to link convolution responses to brightness descriptions. MIDAAS differs from MIRAGE in that each spatial scale generates its own brightness description before a final across-scale averaging. The most serious shortcoming of rule-based models is the need to revise their set of rules (the core of the models) in order to account for other effects. For example, the specification of two-dimensional versions of MIDAAS and MIRAGE given their one-dimensional definition is far from obvious and probably will require new types of rules related to points, corners and terminators (see Watt & Morgan, 1985, p. 1668). An even more serious problem is the fact that a fixed set of rules will often err for new stimuli; Pessoa *et al.* (1995b) discuss a case in point for MIDAAS.

Filling-in

The Pessoa *et al.* (1995b) proposal employs a filling-in account of Mach bands. Filling-in theories of visual perception have been criticized for assuming a form of "look alike" linking hypothesis (Teller, 1980) that is not logically necessary (Ratliff & Sirovich, 1978; Kingdom & Moulden, 1989; Dennett, 1991; O'Regan, 1992). As stated by Burr (1987, p. 1911), "Vision's goal is to extract the essential information about an image, not to produce another image". It should be pointed out, however, that the goal of filling-in theories is not to produce "other images" but to account for the geometric structure of percepts by employing a representational medium that is spatially organized—through the use of spatially organized fields of activity*. The debate on whether filling-in occurs or not (e.g. Coren, 1983; Grossberg, 1983) should concentrate on gathering

*Note also that filling-in theories include "symbolic" stages, such as the ones involved in categorization and object recognition (Grossberg & Mingolla, 1985a, b).

empirical evidence concerning the forms of representation employed by the visual system. Are the underlying mechanisms discrete and symbolic or analog and spatially organized? Note that all of the above models aside from the filling-in scheme produce as their output a discrete sequence of *events*. The output of models such as MIRAGE, MIDAAS and cell assembly (Figs 15, 16 and 17), should not be interpreted as implying patterns over fields of activity; these are only representations of the events detected used by the authors as an aid to the reader. In this context, recent experimental studies on the temporal dynamics of brightness perception by Paradiso and colleagues indicate a process of diffusive filling-in (see below). Pessoa and Thompson (1995) discuss some of the above issues in more detail. They point out that filling-in need not imply Cartesian materialism, or a *homunculus*, and thus should not be viewed as an isomorphism producing internal "images".

Linking propositions for models

In visual science, linking propositions are statements relating perceptual states to physiological states (Teller, 1980, 1984) and provide the logical link between the domains of psychophysics and physiology. They specify the type of mapping that occurs between perceptual and physiological states. For example, Mach bands (psychophysics) have been sometimes explained in terms of the overshoots and undershoots of activity in retinal cells (physiology). Although linking propositions have been historically used for the two experimental domains above, an analogous situation occurs when considering theories and psychophysical (or physiological) results. All models of visual perception need to specify how to link model responses with conscious percept. In this way, several of the issues concerning perceptual–physiological propositions also apply to perceptual–modeling propositions—e.g. the "nothing mucks it up" problem (Teller, 1980). The analogy proposition of Teller (1984) can be adapted directly for modeling:

$$\tau \text{ ``Looks like''} \ \psi \Rightarrow \tau \text{ Explains } \psi,$$

where τ belongs to the domain of model (theory) states and ψ belongs to the domain of perceptual states. In general, the analogy proposition means that if psychophysical and model data can be in some way compared (e.g. plotted on similar axes), then the model can be said to explain the psychophysical phenomenon.

The set of linking propositions employed by the Mach band models above ranges from assuming a spatial resemblance of some model stage with the percept, to postulating that the pattern of rules triggered corresponds to the perception of features, such as lines and edges. However, all models need to more precisely specify the linking propositions, or principles, employed so that they can be evaluated properly. The lack of explicit discussions of linking propositions for models is noteworthy and is an area that needs to be addressed given the large number of existing proposals. This is especially important when theories are used to explain different classes of phenomena.

Multiple spatial scales

All models reviewed are multi-scale theories of early vision. Not all, however, require multiple scales in order to explain Mach bands. The edge-bar inhibition, multichannel, cell assembly and MIDAAS models all employ multiple scales as an integral part of their account of Mach bands. The remaining models do not. Thus, the role of multiple spatial scales in the perception of Mach bands can be used in order to narrow down the types of valid explanations.

Edge-bar inhibition

Ratliff (1984) interpreted his results on Mach band attenuation by adjacent stimuli in terms of the mutual inhibition of bar and edge detectors (Tolhurst, 1972). However, both MIDAAS and the cell assembly model have shown qualitative results consistent with the effect without employing such inhibitory interactions. The filling-in model can also account for the attenuation effect with the behavior of the boundary circuit (including more quantitative fits; Pessoa, 1996). In the model, abrupt luminance transitions such as at a step lead to the sharpening of boundaries (see Fig. 19). In the case of the bar stimuli employed by Ratliff *et al.* (1983), the sharpening triggered by the adjacent stimulus destroys the boundary signals that would normally register the nearby Mach band by the blocking of filling-in (Pessoa, 1996). Thus, the attenuation effects observed by Ratliff *et al.* do not necessarily imply that the inhibition between bar and edge detectors is at work, and in fact is not entirely consistent with the data it tries to explain, as discussed before.

Both the edge–bar inhibition scheme and the local energy model employ even- and odd-symmetric operators in order to explain Mach bands. The main difference is that the former postulates the existence of competition between the two types of operators, while the latter postulates a process of cooperation. Since it has been suggested that inhibitory mechanisms are more vulnerable to monocular deprivation than excitatory mechanisms (Speed *et al.*, 1991), Syrkin *et al.* (1994b) have started comparing the responses of even- and odd-symmetric simple cells in non-deprived and deprived eye cells in an attempt to test the two proposals against physiological data.

Non-linearities

The lateral inhibition account depicted in Fig. 2 is a linear model. All recent models are non-linear. The main non-linearities of MIRAGE and MIDAAS are symbolic and can be expressed as *if–then* clauses as in the classical production system's approach. For example, the bar rule of MIRAGE states that *if* a zero-bounded response distribution occurs with a region of inactivity on both or neither side, *then* a bar is present. MIDAAS employs the interpretation rules illustrated in Fig. 17 depending on the pattern of zero-crossings produced by filtering.

Symbolic if–then clauses provide an effective way to produce a "bifurcation" in the behavior of a system and

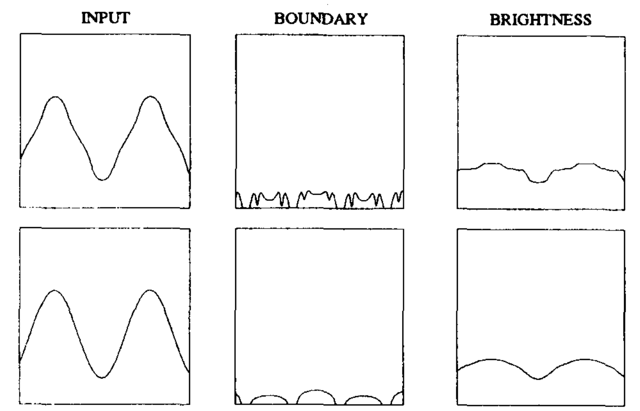

FIGURE 21. Simulations of the filling-in model. Top: simulations of a trapezoidal wave with the Fourier components shifted by $\pi/2$ (shown in Fig. 8). Bottom: simulations of a sine wave for comparison.

generate a reduced set of alternative responses given a continuous input. Other types of non-linearities, or combinations of non-linear stages, are capable of producing similar behavior. The local energy model employs a squaring non-linearity in the determination of energy capable of marking features regardless of contrast polarity. Another key non-linearity is the non-maximum suppression stage which allows only local peaks in the energy function to produce brightness information. Thus only positions containing important features are signaled. Ross *et al.* (1989) point out that interpretation rules, such as used by MIRAGE, are needed to properly disambiguate features indicated or marked by filtering, and that more powerful filtering schemes can obviate the need for such rules. In this context, the non-linearities of the local energy model involved in the combination of even- and odd-symmetric responses, as well as in non-maximum suppression, are responsible for such disambiguation.

The boundary circuit of the filling-in scheme (Pessoa *et al.*, 1995b) also contains several non-linearities, including feedback, which produce one of two distributions of boundary signals: localized or spatially extended. Sharp, localized boundaries are triggered by abrupt luminance transitions and are typically associated with edges (i.e. brightness steps), since filling-in makes the brightness distribution uniform in the vicinity of the edge. Spatially extended boundary distributions originate from shallow luminance transitions and can indicate "features" such as lines. The non-linearities of the model produce a discrete set of behaviors without the explicit encoding of fixed rules.

Both the local energy and filling-in models provide examples of mechanisms capable of generating *categorical behavior without symbolic processing*. Edges are signaled by odd-symmetric responses in the local energy model and are often associated with boundary sharpening in the filling-in scheme. Lines are signaled by even-symmetric responses in the local energy model and often by trapping of diffusion by extended boundaries in the filling-in model. However, the two models do not always agree with respect to the origin of brightness variations. Figure 21 shows a simulation of the filling-in model for the stimulus shown in Fig. 8. The local energy model predicts that the phase manipulation will generate features more similar to edges. However, since there are no sharp discontinuities of luminance in the input, the filling-in model does not produce boundary sharpening. Nevertheless, the resulting boundary signals regulate diffusion in such a way that the brightness variations in the image are well captured*. This brightness modulation should be compared to that produced by a sine wave whose input distribution is similar to the modified trapezoidal wave. The latter stimulus is also modeled accurately by the filling-in scheme (Pessoa *et al.*, 1995b).

Lu and Sperling (1995) determined that the second-order (texture) version of Mach bands (as well as the Chevreul illusion and the Craik–O'Brien–Cornsweet effect) results from full-wave rectification. They were able to show this by demonstrating that the illusion(s) are not perceptible in half-wave stimuli that are neutral to full-wave analysis but become equivalent to luminance stimuli after positive or negative half-wave rectification. They conclude that the perceptual processes governing second-order spatial interactions reflect full-wave rectification. Therefore, their results favor early vision models that employ full-wave, and not half-wave, rectification.

Of the models reviewed, only MIRAGE and MIDAAS explicitly propose half-wave mechanisms; for example, see the third computational step of MIRAGE above. All other models are compatible with the results of Lu and Sperling (although the edge–bar inhibition and multi-channel schemes are not defined in enough detail to be evaluated on this issue). For example, the energy computations of the Morrone and Burr model are a square-law full-wave rectification operation. The filling-

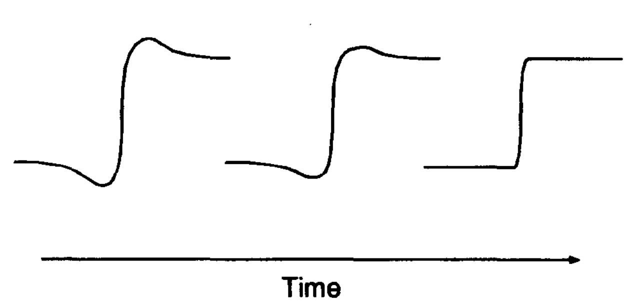

FIGURE 22. Temporal evolution of brightness appearance for a luminance step distribution according to the filling-in model of Pessoa *et al.* (1995b). Initially, Mach bands are seen for a step stimulus (left). As the temporal evolution of brightness processing unfolds, the strength of the bands decays (middle), until, at equilibrium, no bands are present (right).

*This behavior is obtained over a wide range of parameters. The parameters employed were the same used by Pessoa *et al.* (1995b).

in model is interesting as the model includes both full-wave and half-wave mechanisms. Half-wave rectification is performed initially by the generation of ON- and OFF-signals. For boundary generation, such half-wave rectified signals are eventually summed (Grossberg & Mingolla, 1985a, b). This is equivalent to full-wave rectification. However, the half-wave ON- and OFF-signals remain segregated for filling-in and act in an opponent way at the final brightness determination. Thus, the model can also account for what Lu and Sperling refer to as the "normal mode of vision: whites appear white, blacks appear black" (the output of half-wave rectifiers oppose each other). Filling-in models that incorporate both ON- and OFF-channels (Grossberg & Wyse, 1991; Grossberg, 1994; Pessoa *et al.*, 1995b) thus suggest that both types of rectification are necessary to model brightness phenomena. On the other hand, some models have neglected the importance of half-wave mechanisms. One instance is the cell assembly model, which considers only the absolute value of filter responses.

Temporal dynamics

Few investigations of the temporal dynamics of Mach bands are available. With the exception of the filling-in model, the recent theories have been conceived as "static" and thus cannot attempt to model temporal data without further modifications. New experiments exploring the temporal domain are needed in order to indicate how current theories should be extended, or evaluated.

The temporal dynamics of brightness perception is being actively investigated by Paradiso and colleagues (Paradiso, 1991; Paradiso & Nakayama, 1991; Hahn & Paradiso, 1995; Rossi & Paradiso, 1995a, b; see also De Valois *et al.*, 1986). As pointed out, such results have been interpreted in terms of diffusive filling-in mechanisms based on edge information. Some of the results have been modeled successfully by the Grossberg and Todorović filling-in model (Arrington, 1994). In the context of Mach bands, one prediction of filling-in models is that Mach bands should be seen at luminance steps for very brief exposure durations since filling-in, and therefore "homogenization", takes time. More specifically, for brief presentation times the filtering overshoots and undershoots associated with a luminance step do not have the chance to be homogenized by filling-in, and Mach bands should be present (Fig. 22). Moreover, Mach band strength should decay as a function of time.

Is lateral inhibition part of the explanation?

That lateral inhibition is insufficient to account for Mach bands is by now clear. An interesting question, however, is whether such mechanisms are *part* of the explanation. Two lines of evidence suggest that they are. First, the dark-adapted eye does not perceive Mach bands (Békésy, 1968b; Ross *et al.*, 1981) and the appearance of light bands varies as a function of the time of light adaptation (Békésy, 1968b). As discussed, these findings are in line with the modifications in the structure of center-surround retinal receptive fields (Barlow *et al.*, 1957; Enroth-Cugell & Lennie, 1975; Kaplan *et al.*, 1979). Second, the asymmetries between light and dark bands likely reflect differences between ON- and OFF-channels, which remain segregated until cortical visual area V1 (Schiller, 1992). These results favor multistage models of Mach bands in which the outputs of center-surround operators are processed by subsequent stages that eventually generate Mach bands. Among the models reviewed, only MIRAGE, MIDAAS, and filling-in explicitly include center-surround early stages whose outputs are further processed. The other models thus need to show that the inclusion of an early retinal level does not invalidate their main results.

HOW MANY MODELS ARE POSSIBLE?

At first glance, it may seem disturbing that so many different models are capable of accounting for the perception of Mach bands, in some cases with good quantitative fits (Ross *et al.*, 1989; Pessoa *et al.*, 1995). However, when studied closely, several of them share working principles, such as assuming a primitive set of features (lines and edges) or using rules based on the pattern of zero-crossings. The models reviewed here were grouped in three classes: (a) feature-based; (b) rule-based; and (c) filling-in. Feature-based theories postulate that edges and lines are basic primitives of early vision. Rule-based theories may also employ primitive features, but what distinguishes them is a stage of brightness description by the application of a fixed set of rules interpreting what the convolution responses map to. Filling-in theories propose that the spreading of neural activity within filling-in compartments produces a response profile that spatially resembles the percept. According to feature-based and ruled-based models, one of the main tasks of the visual system is to detect salient features (e.g. lines and edges). Most of the "detail" in scenes (e.g. luminance gradients) is ignored. Filling-in theories attempt to build spatial representations that preserve the geometric structure of percepts. Both brightness gradients and sharp brightness transitions are registered. Instead of trying to determine which of the models reviewed here is the "correct" one in the context of Mach bands, it is necessary, as shown in the last section, to evaluate them in the larger picture of visual science and to determine how they contribute to our understanding of vision in general.

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Acknowledgements—The author was supported in part by the Air Force Office of Scientific Research (AFOSR F49620-92-J-0334), and the Office of Naval Research (ONR N00014-J-4100). The author thanks Heiko Neumann, Bill Ross and two anonymous reviewers for many valuable suggestions concerning the presentation of the material in this article. The author also thanks Ennio Mingolla for collaborations in previous research related to the present article and Zhong-Lin Lu for providing material in press.